Field and Laboratory Observations on Microhabitat Selection, Movements, and Home Range of *Necturus lewisi* (Brimley)

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ABSTRACT.— Movements, microhabitat selection and home ranges of 20 adult and 5 juvenile *Necturus lewisi* were studied in the Little River, Wake and Johnston counties, North Carolina, from November 1977 to May 1981. They were tagged with ^{60} Co wires and monitored biweekly. *Necturus lewisi* occupied home ranges ($\bar{x}$ = 17.37m^2 for females and 73.25m^2 for males). Five juveniles tagged and released remained within 134 m^2 over an eight-month period. The primary microhabitat used by both juveniles and adults was loose granite boulders on sand-gravel substrate. The next most important microhabitat was under bedrock embedded in stream banks. Leaf beds, reported to be important habitat for *N. lewisi*, rarely were visited by the animals. Microhabitat use varied with season and temperature range. Trends indicated that dissolved oxygen, flow rate, and precipitation influenced overall movement and microhabitat selection.

Retreat areas were maintained by juveniles and adults in the laboratory, and similar behavior was observed in the field. The animals moved sand and gravel by shoveling with the snout and transporting it by mouth. Retreat areas were defended by adults, who displayed distinct threats and occasional attacks on intruders of either sex. Females permitted males to cohabit their retreats during late winter and early spring, when controlled laboratory temperatures were 8 to 14 degrees C. Larvae and juvenile *N. lewisi* were not attacked and were permitted to enter retreat areas unmolested. Both visual and olfactory cues were used to locate and capture food. The primary method of feeding was to sit at the mouth of the retreat where prey could be detected when it came near. The animals commonly stalked prey at night. Courtship was observed and was similar to that described for *N. maculosus*.

INTRODUCTION

Few studies have been published on *Necturus* behavior, movements, and microhabitat use. Eycleshymer (1906), Smith (1911), Bishop (1926, 1941), and Harris (1961) reported on these topics as observed in northern populations of *Necturus maculosus*. Cagle (1954), Shoop (1965), and Shoop and Gunning (1967) made detailed studies of *N.*

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maculosus and *N. beyeri* in Louisiana. Parzefall (1980) studied behavior in *N. maculosus* and *Proteus anguinus*. Brimley (1924) briefly noted that *Necturus lewisi* was found in leaf beds along fast moving waters. Neill (1963) speculated that *N. lewisi*, like its close relative *N. beyeri*, utilized bottom debris for cover. Ashton and Braswell (1979) provided descriptions of a nest, larvae, and the distinctive post-hatchling larvae, of *N. lewisi*.

The difficulty of capturing or locating animals frequently enough throughout the year to determine general movements, microhabitat use and home range appears to be the reason that such data are not available for *Necturus*. Our three-year study attempted to remove this obstacle by using ^{60}Co tags, following methods described for use in salamanders by Barbour et al. (1969) and Ashton (1975), and in fish by Lee and Ashton (1981). This study was conducted to obtain information on behavior of *N. lewisi* in both its natural environment and the laboratory. Data on biotic and abiotic factors within the microhabitats used by tagged animals were collected and analyzed in an effort to categorize the species' general habitat requirements throughout the year. Observations on microhabitat use, feeding techniques, intra- and interspecific interactions, and growth rates of hatchlings and adults, were made in the laboratory.

METHODS AND MATERIALS

Field Studies

A preliminary study of *N. lewisi* in the Little River, a tributary of the Neuse River in northern Wake County, began in November 1977. The initial purpose was to develop methods of following movements, determining home range, and studying other behavior using radioactive tagging and tracking techniques. Three adults (two females, one male) were caught in minnow traps, some the double-funneled wire type and others employing plastic mesh. Each of the three animals was tagged with two ^{60}Co (35-50 mc) wires injected into the tail musculature. They then were released at the site of capture, at least 20 m from each other.

We initially used a Thyac III survey meter and Model 491 scintillation probe to locate animals. However, with this equipment animals were difficult to detect in more than 30 cm of water, making routine monitoring of movements too sporadic. We also found that animals may move more than 20 m, which necessitated a spatial separation of at least 100 m if we were to recognize individuals without recapturing them. Monitoring problems were overcome by acquiring more sensitive Model 491 waterproof scintillation probes that permitted us to detect animals at any depth at least 80 percent of the time.

From 12 November 1978 through 21 February 1979, 11 adult animals were released at 150 to 250 m intervals along the stream (Site

No. 1). Two-hundred seventy-one positive sightings were made during this period. Nine adult *N. lewisi* were captured and released within the same 25 m² area in Site No. 1 from 15 January 1980 to 28 August 1980. We consequently were unable to identify individuals, but could monitor microhabitat use and movement within the same area under similar stream conditions. Two-hundred seventy-four sightings of tagged animals were made during this period. Similarly, on 21 February 1979 five post-hatchling larvae, 41 to 46 mm total length (TL), were captured by dip-netting, then were tagged and released in the Little River in Johnston County (Site No.2). One-hundred thirty-eight sightings were made of these animals.

All tagged animals were monitored bi-weekly during all three study periods. When a tagged animal was located, data were taken on ambient temperature, flow rate, turbidity, dissolved oxygen, carbon dioxide, and pH, both at the animal's current location and at the site where the tagged animal had previously been found. Standard data were collected at a single control station at each study site throughout the study. This allowed us to evaluate changes in overall stream conditions and compare them with varying conditions in the microhabitat. Weather data, including maximum and minimum air and water temperatures and precipitation, were monitored at or near the control site. Other data were obtained from the U.S. Weather Bureau, Raleigh-Durham Airport, approximately 17 km from Site No. 1 and 27 km from Site No. 2.

The study areas were mapped for depth, bottom types, amount and types of rock cover, and leaf bed development. Very little change in these features took place in both areas throughout the study. General water quality at both study sites was analyzed monthly from April to December 1979 (Table 1). Water analysis was done using a Mach DR-EL/2 with spectrophotometer.

Mercury reached peaks of 4.18 mg/1 ($\bar{x}$=1.07) at Site No. 1 and 5.09 mg/1 ($\bar{x}$=2.17) at Site No. 2. These levels indicated that mercury was a potential pollutant. High levels of nitrates and sulfates were also observed, notably in the May and June samplings, which followed periods of rain and subsequent runoff from surrounding farmlands. Concentrations of all other chemicals tested for were within normal limits.

Two surveys of aquatic invertebrates, one along a transect (Table 2) and the other in a 10 m² quadrat (Table 3), were made at Site No. 1 to quantify potential food items in microhabitats used by *N. lewisi*. Aquatic vertebrates (Table 4) were collected by seine, trap, and electroshock.

Standard SAS programs, including PROC-F reg, categorical data and PROCORR using Perison, Sperman, and Kendall were used to determine significance of specific correlations between behavior and physical factors within the microhabitat. Although tests showed many significant correlations between environmental factors, movement rate,

Table 1. Water chemistry at Study Sites No. 1 (adult study area) and No. 2 (juvenile study area), April-December 1979.

	Site No. 1		Site No. 2	
	Range (mg/l)	$\overline{x}$	Range (mg/l)	$\overline{x}$
cyanide	0.000-0.002	0.002	0.000-0.002	0.002
detergents	0.015-0.048	0.027	0.013-0.033	0.025
iron	0.140-2.520	1.100	0.030-1.800	0.977
mercury*	0.000-4.180	1.073	0.000-5.090	2.175
lead	neg.-0.010	0.002	neg.-0.005	0.002
nitrogen				
ammonia	0.300-0.900	0.641	0.380-1.450	1.110
nitrate	0.300-2.580	0.995	0.000-2.100	0.664
nitrite	0.002-0.050	0.012	0.000-0.013	0.005
phosphorus				
ortho	0.040-0.320	0.176	0.090-0.330	0.180
inorganic	0.010-1.070	0.431	0.090-0.340	0.282
sulfate	0.000-11.000	1.800	0.000-14.400	2.170
sulfide	0.000-0.012	0.003	0.000-0.049	0.019
tannin	0.800-1.820	1.400	0.680-1.750	1.270

*0.002 mg/l is the usual maximum permitted in drinking water

and microhabitat selection, the ranges of comparable data were too broad to make statistically valid statements on their significance.

Laboratory Studies

Larvae and post-hatchlings. — Eight larvae (41-47 mm TL) collected on 21 February 1979 were maintained in 10-gallon aquaria containing 6 cm of aerated water and 2 to 3 cm of sand-gravel substrate. Small stones (x=4 cm²) were provided for cover. The larvae were fed chopped red worms, chicken parts, and occasional aquatic invertebrates and small ranid tadpoles. Growth was measured, and notes on color changes and pattern were made, weekly. Observations were made on feeding behavior, intra- and interspecific interactions, and shelter manipulation.

Adults. — Fourteen adult *N. lewisi* were maintained in the laboratory for from one to three years. They were kept in 50- and 85-gallon aquaria with 4 to 6 cm of gravel substrate and containing granite rocks (6-15 cm diameter) for cover. Four sets of 80x80x4 mm double plastic plates were used as artificial cover. The top plate was sprayed with black latex paint to block light, while the bottom plate was clear. The black plate could be removed with little friction to permit observation of animals.

The study aquaria were maintained at 15° to 26° C ($\overline{x}$=24° C) during the first year. A temperature control unit used during the last two years of the study permitted us to maintain variable water temperatures equal to those observed at Site No. 1 (R=3°-24° C, $\overline{x}$=16° C). Light sources were north-facing laboratory windows and overhead fluorescent fixtures. Light duration and intensity could not be controlled, but duration was similar to normal seasonal day length. A red light was used for some night observations.

DESCRIPTION OF STUDY SITES

Site No. 1

Site No. 1, where we studied adult *N. lewisi*, was located on Little River at Mitchell's Mill Pond State Park, northern Wake County. This was the same site used by Fedak (1971) during his study of the same species. Little River is a headwater stream in the Neuse River drainage of northeastern North Carolina. The stream begins on the Piedmont Plateau and confluences with the Neuse River just after crossing the Fall Line Zone.

Little River at Site No. 1 is a typical Piedmont stream; 30 percent of the bottom and 8 percent of the banks are covered with granite boulders and outcrops. The remainder of the stream bottom was sand and fine gravel. The banks were steep, with a 3:1 or greater slope, and consisted of sandy-clay soil. The banks were profusely pocked by burrows of crayfish and other animals. On the high-energy side of the stream the banks were undercut in a number of places, and burrows of *Castor* and *Ondatra* were present in some. An average of 72 percent of the main study area was shaded by the surrounding mixed deciduous forest. Mean width of the stream at the control site for this area was 7 m, and mean depth was 1.2 m. The greatest depth recorded was 1.9 m, although we estimated that water level may have reached a height of 2.4 m during severe flooding. The shallowest depth recorded at the control site was 0.6 m. Water temperatures at the control site ranged between 8° C and 22° C during the spring and 1° C to 12° C during the winter. The greatest change in water temperature between sightings (48 hr) was 5C°. Dissolved oxygen levels ranged between 4 ppm and 9 ppm ($\overline{x}$=7.2 ppm). Turbidity ranged from 14 to 40 ftu (x=30.25 ftu). Mean non-flood rate at the standard site was 4.9 cm/second.

Site No. 2

Site No. 2, where we studied larvae, was in the Little River, northwestern Johnston County, 12.8 km east of Site No. 1. This site lies within the transitional Fall Line Zone between the Piedmont Plateau and the Coastal Plain, as indicated by the lack of granite outcroppings, presence of sandy soils, and paucity of large rocks in the river bottom. Cypress trees, common along the river bank, were absent from the study site itself. Twenty percent of the sandy bottom within Site No. 2 was

Table 2. Transect invertebrate survey, 19 April & 13 June 1980, Study Site No. 1. (No./m^2 by microhabitat.)

Habitat	Bank Area		Gravel-Sand		Gravel-Sand		Swept Sand		Sand-Granite Rock		Bank Granite Rock	
Date	April-June		April-June		April-June		April-June				April-June	
Odonata*												
Gomphidae	1	7	5	2		6			1	1	5	3
Libellulidae		3		1				1			3	4
Macromiidae	2	4	2				2		6		1	
Coenagrionidae	2	1	1		1			1			3	3
Ephemeroptera*												
Ephemeridae			2				2				1	
Ephemerellidae		1	1				2				4	1
Heptageniidae								3				
Trichoptera*												
Mollannidae			1			1	2	2				
Limnephilidae								3			1	1
Philopotamidae		1										1
Polycentro-podidae								2				1
Coleoptera*												
Hygrobiidae			1									
Diptera*												
Chironomidae*		13		23		1	1			5	2	3
Simuliidae*						8						

Megaloptera*												
Sialidae						1		1		1	2	3
Crustacea												
Isopoda*											1	
Pelecypoda*												
Sphaeriidae								1	1		6	4
Unionidae		1										1
Gastropoda												
Viviparidae		15				7		13	4	2		4
Physidae*			2					1				
Annelida												
Lumbricidae*	1								2			
Glossiphonidae												
Oligochaeta*				1		1						
Diplopoda*											8	

Table 3. Quadrat invertebrate survey in microhabitats in primary study site, 19 April 1980 (number by habitat).

Order-Family	Bank, roots, floating detritus	Substrate under rocks sand-gravel	Open water seine-detritus	Rock surfaces	Leaf bed (seining)
Odonata*					
Libellulidae	1	5		4	4
Gomphidae	10	6	1		6
Macromiidae	8	5	7	1	
Aeshnidae		1			
Cordulegastridae			1		
Coenagrionidae	4	7			1
Calopterygidae		1			
Ephemeroptera*					
Ephemeridae		1			2
Ephemerellidae	2			4	
Heptageniidae	1	1		178	
Trichoptera*					
Leptoceridae	2			1	
Psychomyiidae	1				
Philopotamidae		1		2	
Lepidostomatidae				5	
Polystoechoridae					
Coleoptera*					
Staphylinidae				1	
Dytiscidae*				1	

Diptera*					
Chironomidae			1	8	13
Crustacea					
Palaemonidae	3	1	6		
Cambaridae	6	14	1		3
Amphipoda*				1	2
Arachnida					
Araneidae	1			1	
Clubionidae		1			
Annelida					
Oligochaeta*		1		1	
Glossiphonidae					2
Lumbriculidae*					
Gastropoda					
Viviparidae	2			3	56
Physidae*		1		1	
Planorbidae				3	
Pelecypoda*					
Unionidae	2	1		1	6

*Invertebrate taxa used as food items (see Braswell, this issue).

Table 4. Aquatic vertebrates collected or observed in Study Site No. 1 (1978-80).

Fishes	Amphibians	Reptiles
Acantharchus pomotis	*Amphiuma means*	*Pseudemys concinna*
Anguilla rostrata	*Desmognathus fuscus*	*Sternotherus odoratus*
Aphredoderus sayanus	*Eurycea bislineata*	*Nerodia sipedon*
Esox americanus	*Necturus punctatus*	
Erimyzon oblongus	*Rana catesbeiana*	
Etheostoma olmstedi	*Rana clamitans*	
Etheostoma vitreum	*Rana palustris*	
Gambusia affinis	*Acris gryllus*	
Ictalurus natalis	*Bufo terrestris*	
Lepomis auritus		
Lepomis cyanellus		
Lepomis gulosus		
Lepomis macrochirus		
Micropterus salmoides		
Nocomis sp.		
Notropis altipinnis		
Notropis amoenus		
Notropis procne		
Notropis sp.		
Noturus insignis		
Percina peltata		
Percina roanoka		
Umbra pygmaea		

covered by small, flat, granite rocks with individual surface areas of not more than 0.5 m^2. Smaller flat, granite rocks ($\bar{x}$=8 cm diameter) covered approximately 15% of the bottom. Ten percent of the study area was commonly covered with leaf beds during fall through early spring months. The stream banks had a 2:1 slope, and were commonly undercut and pocked with numerous animal burrows.

Mean width of the stream at the standard control site for this area was 13 m, with an average depth of 1.5 m. The greatest increase in depth recorded was 2.4 m, although greater depths may have been obtained during severe flooding when monitoring was not possible. The shallowest depth recorded at the control site was 48 cm, with seasonal fluctuations averaging $\pm$34 cm. Water temperatures at the standard site ranged from 1° C to 21° C with seasonal fluctuations in temperature similar to those at Site No. 1. Dissolved oxygen levels ranged from 5.4 ppm to 8.0 ppm ($\bar{x}$=7.2 ppm). Turbidity levels of 16 to 40 ftu ($\bar{x}$=31.5 ftu) were recorded. Table 1 summarizes the physicochemical data for both sites.

RESULTS

Movements and Home Range of Adults

Of nine adult *N. lewisi* tagged in the first year, five were located frequently enough (80% of all attempts) to permit measurement of home range. However, even the tagged animals that were not located this frequently appeared to move within a home range pattern. The size of the ed by calculating the area within the outermost points of movement and eterminwithin which 95 percent or more of all movements took place (Table 5). Animals monitored in the second year, which were released within a 25 m^2 area, showed that home ranges overlapped regardless of sex or season. Throughout the year all males made greater individual movements ($\bar{x}$=75.4 m) than females ($\bar{x}$=17.5 m). Females displayed a mean home range of 17.37 m^2 while males had significantly larger home ranges, $\bar{x}$=73.25 m^2 (Table 5).

Table 5. Home range and movements by adult *Necturus lewisi*.

Specimen No.	Sex	Home range (m^2)	Movements % 0-1 m	Movements Max.	Movements $\bar{x}$
1	♀	18.75	82	85	4.10
2	♂	84.75	62	425	100.00
3	♀	16.00	53	250	27.00
4	♂	90.00	88	210	86.60
5	♂	49.00	41	185	63.80

Each home range contained bank areas with animal burrows or rock overhangs, large flat rocks over a sand-gravel substrate, and slack water areas where leaves and other debris formed detritus mats during the fall and winter. Water depths ranged from 15 to 160 cm ($\bar{x}$=73 cm) (Table 6). We attempted to determine if movements of all animals changed with environmental factors such as rainfall, barometric pressure, moon phase, and air temperature. Seventy-two percent of all adult movements took place within 24 hours after a rainfall of 9 mm or more. Movements declined, however, when rainfall exceeded 40 mm. When stream level increased by more than 15 cm, little movement was observed unless the greater depth was maintained for more than 7 days. In any season there was a 64 percent increase in overall movements as barometric pressure fell or remained below 29.9 mm. Movements increased when moon phase changed from full to dark. Overall movements increased during the spring and fall and declined during the winter and summer.

Movements correlated with overall stream and microhabitat temperature changes. Carbon dioxide levels and pH remained relatively

Table 6. Characteristics of microhabitats used by tagged adult (Study Site No. 1) and juvenile (Study Site No. 2) *Necturus lewisi*. (* = flow rate below measurable level but some flow evident.)

	Temperature (C)		Flow rate (cm/sec)		Oxygen (ppm)		Depth (cm)		Substrate type (%)[a]				
Adults	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	1	2	3	4	5
summer (Jun-Sep)	23-30	27.3	*k* 0-7*	1.34	5-8	6.2	160-25	74.7	18	68	0	14	0
fall (Oct-Nov)	3-8	3.6	*k* 0-4	1.57	7-9	7.8	105-40	55.6	10	80	0	0	10
spring (Mar-May)	15-26	20.5	*k* 0-33	7.55	7-9	7.9	160-15	78.7	49	49	0	2	0
	1-14	6.7	*k* 0-40	14.79	6-9	7.8	127-17	72.5	52	33	0	15	0
Juveniles													
summer	18-27	22.1	*k* 1-19	3.63	4-7	6.1	25-150	104.7	10	99	0	0	1
fall	13-20	17.6	*k* 5-39	18.67	7-9	7.7	140-150	146.6	0	100	0	0	0
spring	12-22	16.6	*k* 1-40	13.66	7-9	7.8	50-225	141.7	14	67	0	2	17

[a] substrate types:
1 = under bedrock or large slabs of granite imbedded in bank
2 = loose granite rocks or boulders over sand-gravel substrate
3 = small rocks (*k* 5 cm dia.) in or on gravel substrate
4 = clay or soil banks
5 = leaf beds

constant between the control site and any microhabitats used by *N. lewisi*, and had no apparent bearing on movement.

Winter Movements and Microhabitat.— During winter, adult *N lewisi* were found either under large granite rocks or in burrows in the bank 85 percent of the time. Mean water temperature was 6.7° C. Of all movements made during this period, 29 percent were to microhabitats that were 1 C° or more higher than the standard site temperature (Table 6), and 28 percent were to microhabitats with higher levels of dissolved oxygen (7-9 ppm) and higher flow rate ($\bar{x}$=14.79 cm/sec). A decline in overall number of movements was noted for all animals by 67 percent. When the stream temperature dropped below 4° C, movement was to areas where groundwater entered that was 2 to 4 C° higher than the standard site temperature. No sexual difference in frequency of movement was observed during the winter period.

Spring Movements and Microhabitat.— Between March and May the number of movements was 48 percent greater than in all other seasons. Generally, as temperature increased to 8° C, females showed increased (27%) movement. At 14° C, female movement declined but overall male movement increased. This period of increased male movement coincided with expected breeding and nesting periods. Thirty-six percent of movements made during this period were to microhabitats with higher O_2 levels ($\bar{x}$=7.9 ppm) and 34 percent were to areas of greater flow ($\bar{x}$=7.8 cm/sec). The primary microhabitats used during period this were considered suitable nesting sites (Ashton and Braswell 1980). The microhabitats used 98 percent of the time by both sexes were large bedrock outcrops or large boulders with sand and gravel beneath them.

Summer Movements and Microhabitat.— Generally, summer movements by both sexes, with an overall decline of 40 percent in frequency, were to microhabitats that had lower temperatures (34%) and higher oxygen levels (37%) (Table 6). The use of granite boulders and outcrops in the main flow of the stream increased during this period.

Fall Movements and Microhabitat.— The overall river environment, including the microhabitats used by *N. lewisi*, was relatively uniform in temperature, oxygen levels, and other physical factors. General movements were from the main flow to the winter retreat areas.

Movements and Microhabitats of Larvae and Post-hatchlings

Since five post-hatchlings were captured and released in the same area, movements by specific individuals could not be determined. All, however, remained within a 134 m^2 area. At no time were two tagged individuals found under the same cover, but it was not uncommon to find three or more individuals within one square meter of one another.

The primary habitat used by juveniles consisted of granite boulders, 0.5 m diameter, with underlying sand-gravel substrate. Movements into leaf beds were rare (only two sightings) until early spring, when 17 percent of all sightings were made in this habitat. The beds that salamanders used were formed over a mud bank on the low-energy side of the river. During this period, leaves were intact or only slightly decomposed, and many potential food invertebrates were present in the leaf litter.

Captive Behavior

Retreats.— As did tagged animals in the field, captive *N. lewisi* used rocks for cover or hid under artificial plexiglass plates when rocks were not provided. Development of a retreat began within 24 hr after the animal was placed in an aquarium. Retreats were made under cover by moving the underlying sand and gravel to either side of the developing cavity, or by forcing it from under the rock. Substrate was removed by shoveling or pushing with the snout and head. Excess sand and gravel was moved through an opening that eventually became the main opening to the cavity. This excess material formed an elliptical shelf directly in front of the opening. The cavity itself usually was oval in shape, and had a diameter measuring approximately two-thirds the total length of the animal.

Once developed, the retreat area was maintained by the attending animal. Gravel and sand were occasionally moved from the cavity by mouth or by shoveling with the snout. Oral intake of gravel was observed in three females and one male. The pieces, approximately 3 mm diameter, were moved to the shelf in front of the main entrance and expelled from the mouth with some force. A female was observed repeatedly picking up the same piece of gravel in the mouth, then placing it in a different location each time (like a bird placing sticks in a nest). The shelf areas of all captives were maintained devoid of algae and any other debris that commonly formed on surrounding gravel. The rock surface directly over the cavity was similarily maintained.

In order to test cleaning behavior (?) by *N. lewisi*, flat granite rocks with algae encrusted upper surfaces were collected from the Litte River. They were then placed in a tank, on sand and gravel substrate, with their encrusted surfaces facing down. Three adult *N. lewisi* were released into the tank and established residence under the rocks. Within 48 hr, the area of rock undersurface that covered each retreat was clear of algae.

In microhabitats used by "tagged" animals in the field we on several occasions observed similar retreat area maintenance. When animals were under broken granite rocks the opening was always on the downstream side of the rock. The shelf area in front of the opening was developed in a fashion similar to that previously described, and the underside of the rock was devoid of encrustation.

Retreat development in larvae was not evident, although individuals repeatedly used the same rocks. Retreat development was apparent in juveniles of more than 47 mm total length. The post-hatchling larvae abandoned their retreats if larger rocks were placed in the aquaria. Adults, however, remained in their original retreats even when additional cover was provided. Exceptions to this behavior were seen only in those adults that were originally provided with plastic plates alone. They would move to rock cover within 24 hr after it was introduced.

Feeding.— All captives were fed twice weekly and maintained on a diet of earthworms, chopped chicken hearts, and live invertebrates, along with occasional ranid tadpoles and minnows.

Both juveniles and adults displayed two feeding techniques. Most commonly, an animal would lie in wait with snout protruding at the opening of the retreat. Any organism or small object moving with the flowing water that crossed the shelf area stimulated an alert response from the attending animal, which flared its gills and moved partly out of the opening. The second feeding technique was to actively search the bottom of the tank. This was done primarily at night but sometimes during the day. Distinct color fading was observed in striped post-hatchling larvae when they were actively feeding at night. This fading was so acute that their dark sides completely faded to gray-brown and were indistinguishable from the light brown dorsum.

Both sight and olfaction apparently play an important role in locating food. Movement of prey could be discerned at least a meter away. Movement of potential prey also stimulated, but was not necessary for, an attack to be initiated. Feeding animals seemed to respond to very slight movements when the prey was within 5 cm.

Olfactory response to food was tested by dropping chopped earthworms and chicken hearts at varying distances downflow and out of the field of sight of the test animal. In 10 tests, where food was 1 m from it, the animal responded within 32 to 125 seconds ($\overline{x}$=47 sec). Response was marked when the animal raised its head approximately 45 degrees from the surface. As it walked towards the food, the animal would stop and repeatedly put its snout to the substrate until it reached the food. Other foods dropped on the shelf about 10 cm beyond the waiting animal stimulated a similar response. Juveniles and larvae did not respond to nonliving food dropped away from the entrance to their retreat areas. Their response seemed to be stimulated by sight.

Active stalking of prey occurred at night. Prey included earthworms, *Eurycea* larvae, tadpoles, and the fishes *Notropis*, *Etheostoma*, and *Umbra*. The mudpuppy would walk slowly in the direction of the prey, pausing frequently and putting its snout to the substrate. When within striking distance, ca. 2 to 3 cm away, the animal would stop, apparently watching the prey. At the slightest movement the mudpuppy would engulf the prey with a rapid pharyngeal intake similar to that described in *Gyrinophilus* (Bishop 1943; Cooper and Cooper 1968). A 4 cm earthworm or 3 cm fish would be totally and instantly engulfed, then swallowed. Larger prey were often regurgitated and re-swallowed two or more times before they were ingested whole. When larger prey was taken, the mudpuppy would return to its retreat before regurgitating and swallowing occurred. Fish were swallowed tail first. There was no indication that the mudpuppies had difficulty with fin spines or the sharp operculum of *Etheostoma*. The largest *Notropis* swallowed was ca. 4 cm long. Fish were captured at night as they settled on the bottom. The mudpuppy would stalk the intended prey, "freezing" each time the fish moved, until it was within striking distance.

Courtship.— Courtship was observed only once, on 8 March 1979. The female (146 mm SVL) had been in captivity three months. The male (106 mm SVL) was released into the tank within two hours of capture. Within twenty minutes after the male was introduced courtship was in progress. Initial contact between the two was not observed, but apparently began at the female's retreat rock. The courtship took place within a 1 m^2 area and continued for nearly an hour. The female was first observed crawling slowly over the substrate with the male following ca. 2 to 4 cm from her tail. The male would frequently touch its snout to the surface. When the female stopped moving, the male moved forward and positioned its snout just behind the rear leg of the female. During this initial pursuit the female's gills were distinctly flared while the male's were held close to the neck (Fig. 1).

The female remained motionless, and the male moved across her body at the base of the tail. Once their bodies were parallel, the male began to stroke or rub the female with his chin. Stroking began on the top of the head, and the male moved his chin posteriorly along the female's neck and mid-dorsum, then back to the head. This stroking movement occurred twelve times in five minutes. Each time the male's chin came into contact with her neck or head, the female would raise her head from a position parallel to the substrate to an angle of 30 degrees or more; her body was held rigid. At this point the gills of both animals were flared and rapidly pulsating (Fig. 2). The entire chin-rubbing phase lasted a total of 18 minutes with actual rubbing occurring sporadically at intervals of a minute or more. The stroke pattern shortened in length to where the male's chin moved from first behind the head onto the neck region. During this and subsequent phases, the female remained motionless and kept her head slightly erect.

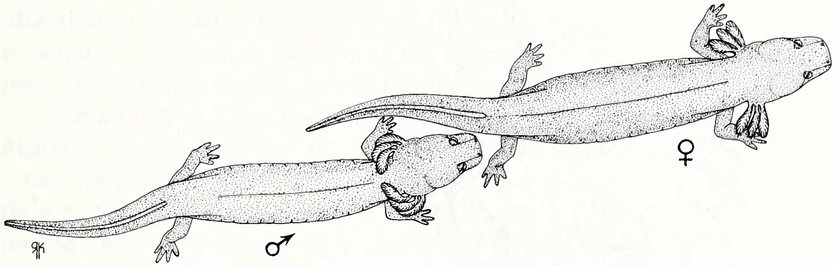

Fig. 1. Initial pursuit by male of female during courtship.

During the second phase the male slowly circled the female in a clockwise movement. During circling, body contact was maintained with the female (Fig. 3). As the male moved in front of the female her head became more erect. Three complete circles were made by the male in six minutes.

The courtship display ended when the male, on the third circling, came into a parallel position with the female. The sides of their bodies were touching, with the male's hind and foreleg resting on the female's dorsum and their heads and tails parallel (Fig. 4). Both animals remained in this position for more than 30 minutes, after which they retired to the

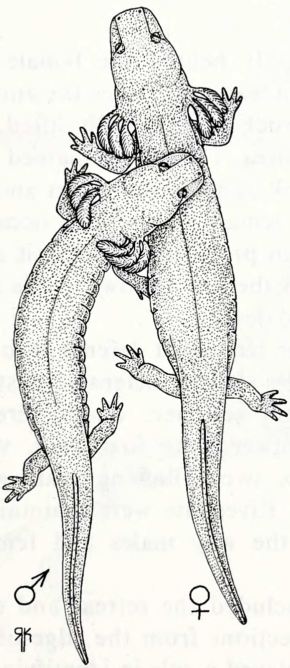

Fig. 2. Chin rubbing by male over head and dorsum of female.

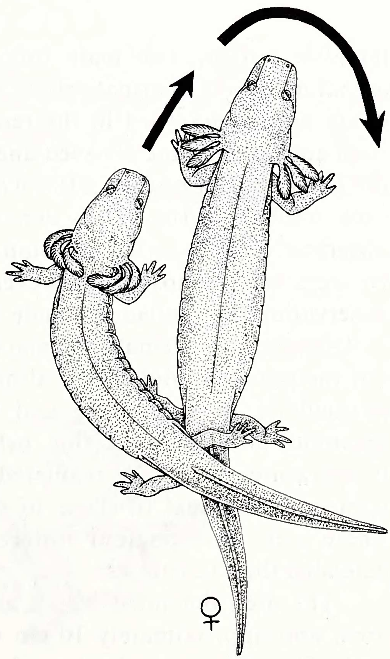

Fig. 3. Male circling female.

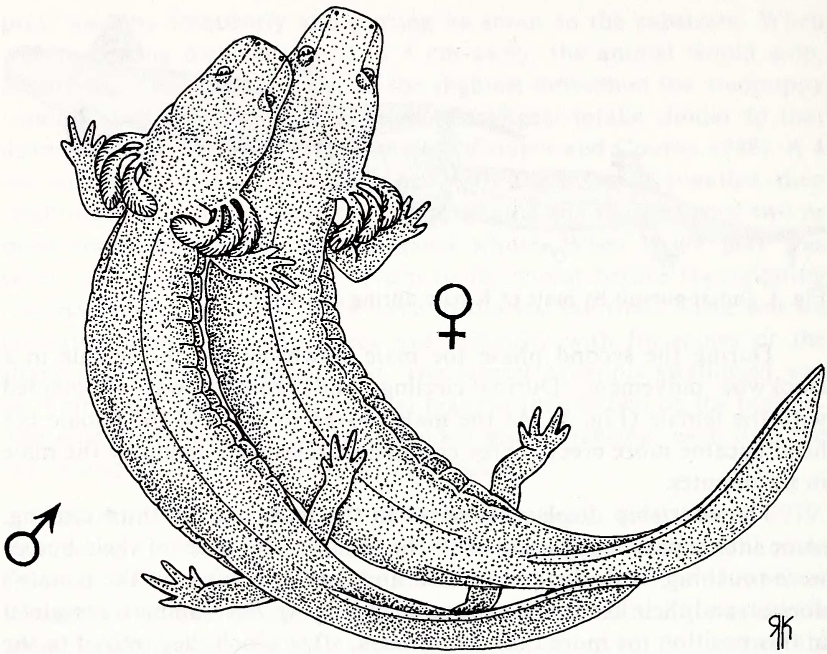

Fig. 4. Male lying next to female; note position of legs.

female's retreat. The male followed directly behind the female. No actual mating or spermatophore deposition was seen. Since the animals could not be observed in the retreat the rock was carefully lifted, but both animals became alarmed and left the area. The male remained with the female for three days, after which it took up residence under another rock. Following the male's departure the female was on one occasion observed in an inverted position as though preparing to deposit eggs. No eggs were deposited, however, and on the day following this final observation the egg-laden female was found dead.

Aggression.— Females displayed greater territorial defense throughout the year than did males, although males showed defensive postures particularly in late spring and throughout summer. There were no apparent differences in this behavior between the first year, when temperatures were not regulated, and the two following years when temperatures equal to those of the Little River site were maintained. There were no apparent differences in the way males and females defended their territories.

The area defended by all animals included the retreat and shelf area, and approximately 10 cm in all directions from the edge of the rock. There was no indication that scent played a role in identifying an intruder; the resident responded only when visual contact was made.

There was some indication, however, that intruders may have used olfaction in identifying an occupied territory. An intruder would touch its snout to the gravel shelf or at the entrance. If the retreat was occupied, the intruder usually moved hastily away from the area.

An animal in residence when an intruder approached made a threat display. Upon observing the intruder, the resident moved out of the retreat opening so that its head and gills were exposed. The gills would flare to the maximum level and slowly pulsate (Fig. 5). If the intruder moved away or stopped, the resident would retreat into the opening. If the intruder instead moved toward the entrance or approached the shelf area, the threat was repeated. The resident would move out of the retreat if an intruder was on the shelf or close to the opening. At this time the resident's gills would be flared and rapidly pulsating, and occasionally its upper lip would be curled (Fig. 6). This was done quite rapidly, and usually indicated that an attack was imminent. This lip curl display also was quite commonly seen when adult animals were handled, but no animals ever attempted to bite during capture or handling.

Attacks occurred in at least 50 percent of all intrusions observed. Intrusions were quite rare, however, except when food or a new animal was introduced into the tank. An attack would occur quite rapidly after repeated threats and false charges. The resident animal would charge

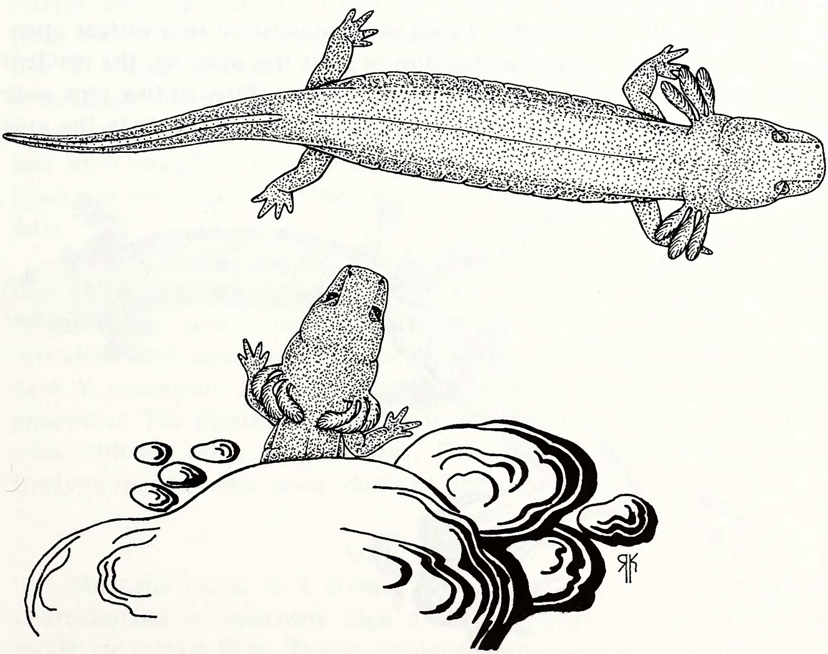

Fig. 5. Initial threat display to intruder by resident animal.

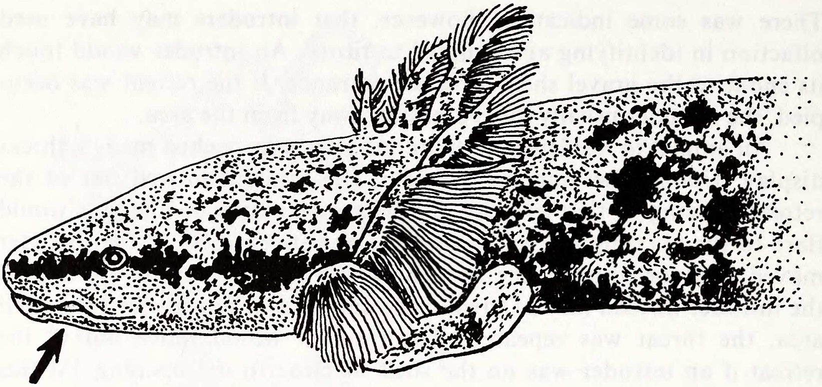

Fig. 6. Lip curl or flash. Upper lip is turned upward, revealing light underlying tissue; gills flared.

forward and bite the intruder. Seventy percent of the bites were at the base of the tail (Fig. 7), but some were just behind the foreleg. The bite caused a circular wound of numerous lacerations, which usually left a gray-white scar. Contact was fast and brief, and no attacking animal was observed to hold onto its victim. A second or third bite was sometimes delivered as the intruder moved away. At no time was an intruder seen to defend itself.

Occasionally an intruder would move unnoticed to a retreat opening. If the intruder placed its head in or near the opening, the resident animal would instantly bite the intruder's snout. Bites of this type were similar to those previously described. The bite would include the area

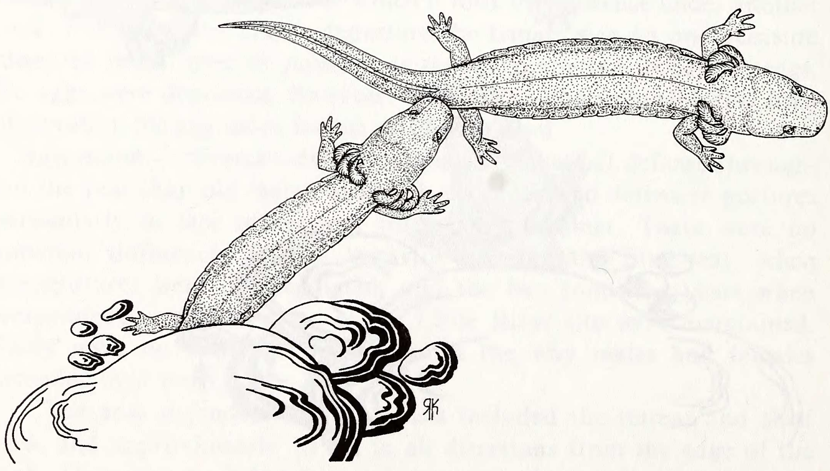

Fig. 7. Attack, with biting at base of tail of intruder.

around the nostrils dorsally and the anterior end of the lower jaw ventrally. It was not uncommon for the intruder to thrash about while pulling its head from the opening of the retreat.

Two larvae 49 mm and 51 mm TL, and two striped juveniles, were introduced into a tank occupied by an adult so that adult-larval interactions could be observed. Larvae were tolerated, and could venture into retreats of either males or females. The adult animal became aware of the larvae, possibly as potential food items, and often stalked them for short distances. At no time, however, was a larva eaten, even when left in the adult tank for two days. Gary Woodyard (pers. comm.) reported a captive adult eating a juvenile, but the adult was not being regularly fed.

Two adults, a male 84 mm SVL and a female 95 mm SVL, and two subadults, 62 and 59 mm TL, of *Necturus punctatus* were released into a tank with an adult *N. lewisi* to observe interspecific interactions. The two subadult *N. punctatus* were immediately eaten. The adults were attacked by resident *N. lewisi*, even by individuals that were somewhat smaller in body size than the *N. punctatus*. During these attacks the threat displays were the same as previously described, but the biting was distinctly different. Interspecific bites were directed to the head and gills of the intruder. The attacker would grasp the victim until it thrashed loose. On one occasion, an intruding *N. punctatus* was dragged to the retreat opening and held there for several minutes. During this time there was violent thrashing, including a rolling or spinning motion by the *N. lewisi*. Wounds from these bites appeared to be much more severe than those inflicted on intruding *N. lewisi*. Deep lacerations were always evident, and covered the entire head and gill rakers if the head had been engulfed, or were across the snout and throat region if the head was not engulfed. These wounds often became infected and were fatal.

Two *N. lewisi*, one juvenile 52 mm TL and one adult female 118 mm SVL, were introduced into a 10-gallon aquarium where two adult *N. punctatus* were in residence. No attacks by the residents or by the intruders were seen, although the *N. lewisi* went under rocks with resident *N. punctatus*. After one night the adult *N. lewisi* displaced one *N. punctatus*. The displaced animal moved under, and remained under, the rock with the other *N. punctatus*. The juvenile *N. lewisi* was moving freely in the tank and never observed under rocks.

DISCUSSION

Necturus lewisi is a stream salamander that uses microhabitats characterized by relatively high dissolved oxygen concentrations and moderate stream flow. This is similar to other species of southern *Necturus* that have been studied, including *Necturus beyeri* and *Necturus* *maculosus*, but considerably different from the wide spectrum of aquatic habitats used by northern *Necturus*. The two primary microhabitats used by *N. lewisi* in Piedmont Plateau environments are broken metamorphic or granite rock over sandy-gravel bottoms, and along stream banks where there are rock outcroppings. This is contrary to the findings of Fedak (1971), who stated that leaf beds are of primary importance. We found that leaf beds are only occasionally visited, probably on feeding forays. Use of burrows or rock outcroppings is primary and similar to those described by Neill (1963) for *N. beyeri*.

Rock microhabitats do not occur in the Coastal Plain range of *N. lewisi*, and further studies of its ecology should be conducted in this province. We can speculate, however, that bottom debris, roots, and bank microhabitats replace rocks, and high oxygen levels and flow are important factors in microhabitat selection. In any case, it would appear that damming, stream clearing (snagging), or channelization would be detrimental to *N. lewisi*.

Home ranges were observed, using tagged animals, and are similar in size to those that Shoop and Gunning (1967) alluded to in their mark-recapture studies of *N. maculosus* and *N. beyeri*. It appears that male *N. lewisi* have a larger home range than females, and that they have different and longer periods of movement. Changes in movement and microhabitat use appears to be seasonally regulated by temperature and rainfall. Environmental data were not collected in a way that would provide statistically valid analyses.

Periodic high levels of mercury and other potential pollutants could have long range effects on *N. lewisi* populations. However, there are no data to show what these effects may be or at what concentrations detrimental effects take place (R. Hall, pers. comm.). The availability of such data would be important in evaluating future conservation status of *N. lewisi*.

Microhabitats are manipulated by *N. lewisi*. The animals actively develop a retreat under cover and maintain the area free from algae and debris. This was observed in the laboratory and in the field. The method of cleaning sand and gravel by taking it into the mouth has not been reported for this genus.

Pairing was observed in captive males during the breeding period, and the more aggressive females permitted males to use the same retreat areas at this time. Ashton and Braswell (1979) reported a male under a nest rock and speculated that both males and females may participate in nesting.

Agonistic behavior increased between individuals after the nesting season. Threat displays in both sexes include flared and waving gills, and lip curls. When two *N. lewisi* are involved, false attacks are often displayed prior to actual contact. This is followed by a bite that appears to cause little damage to the intruder. Attacks on *N. punctatus*, however, were more direct and resulted in serious wounds or death.

Parzefall (1980) reported that *N. maculosus* and *Proteus anguinus* responded to olfactory cues in water and those left on substrates. *Necturus maculosus* recognized and avoided retreat areas occupied by *Proteus*. *Necturus lewisi* displayed similar responses to retreats that were not physically occupied by the resident. This indicates that similar olfactory cues may be involved in identifying territory. Adult *N. lewisi* recognized larvae and juveniles and did not display territorial aggression nor did they attempt to eat them.

Necturus lewisi was much more aggressive than the syntopic *N. punctatus*, which never challenged intruding *N. lewisi*. Captive *N. punctatus* were displaced by *N. lewisi*. This may indicate an amensalistic relationship in the wild.

Courtship in *N. lewisi* was similar to that reported for *N. maculosus*. Bishop (1941) observed that the courting male repeatedly crossed over the female, which became motionless with head erect, but he did not report chin rubbing or trailing as was observed in *N. lewisi*. These may indicate that pheromones, as well as the tactile senses, play an important sexual role. The actual transfer of spermatophores from male to female is still unobserved in *Necturus*.

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